Modeling the past and contemporary habitat suitability and distribution of the Levantine viper *Macrovipera lebetinus* (Linnaeus, 1758) (Ophidia: Viperidae)

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**Abstract**

Evaluating the climate changes in the past and contemporary times, and the impact of those changes on the distribution range of the species has attracted research interest. The venomous snakes of the genus *Macrovipera* consisting of the recognized species *M. lebetinus* and *M. razii* are documented from Iran. In this study, we modeled the potential distribution areas and determined the suitable habitats in the past (the Last Interglacial [LIG], and mid-Holocene [MH]), and their present distribution for the Levantine viper *M. lebetinus* by MaxEnt. Models of the species indicated good fit operation by the average high area under the curve (AUC) values (LIG = 0.979 ± 0.008, MH = 0.968 ± 0.028, Contemporary = 0.933 ± 0.036). Three important climate variables had significant contributions to the simulation of the LIG model distribution of *M. lebetinus* as mean temperature of the driest quarter of the year (43.8%), isothermality (26.9%), and mean temperature of the wettest quarter of the year (17.9%); the maximum temperature of the warmest month (36.4%), mean temperature of the wettest quarter of the year (25.2%), and isothermality (21.2%) variables had significant contributions to the contemporary time and the MH model distribution the Levantine viper, respectively; Two important climate variables had immense contributions to the prediction of the contemporary model distribution *M. lebetinus* as seasonal and annual precipitation (32.9%), and a topographic variable as slope (31.5%). Because it seems that they have sensitivity to temperature and precipitation levels of the seasons. The MH and the LGM models indicated a larger suitable area than the contemporary distribution, and it is concluded that these variables form a natural barrier for species dispersion.

**Keywords:** Blunt-nosed viper, Climate condition, Last interglacial, mid-Holocene

**Introduction**

The portentous response of species to the continuous climate changes may be incessantly *in situ* at their tolerance limits or changing ranges in the regions where the climate is within the species
tolerance limits, and ultimately extinction (Davis et al., 2005). The glaciations were interrupted by interglacial periods (Ray, 1992), the climate warming caused the forests to be revived in the areas where once supported tundra vegetation (Sillero & Carreterob, 2012), and climate of the Last Interglacial period (LIG: 150,000–115,000 years BP) was warmer than the present time with an increased temperature gradient (~3-5 °C) in polar regions towards lower latitudes and caused the sea-level to rise (approximately 4 to 6 m) and the ice sheets to reduce (Pickarski, 2014; Nikolova et al., 2013). During the mid-Holocene (6k), summer temperatures were warmer than the present time in the high latitudes of the Northern Hemisphere, but northern Africa, Arabia, and southern Asia (Iran and surrounding regions) underwent the conditions that precipitation and humidity increased compared to the present time and these conditions resulted in both African and Asian monsoons (Wanner et al., 2008; Jones et al., 2013). Species distribution models (SDMs) can be capitalised on to investigate the impingement of climate changes on the distributions and abundances of species (Thomas et al., 2004); analysing SDMs can assist in conserving management planning (Graham et al., 2004, Farahani and Asgharzadeh, 2023), understanding theoretical research on ecological processes (Phillips et al., 2009), determining biogeographical patterns, predicting potential distribution (Ananjeva et al., 2006), appraising possible future changes in the diversity (Ramirez-Villegas et al., 2014) and predicting potential distribution and habitat suitability for species (Karamiani et al., 2018). MaxEnt is a general approach for characterising the probable distributions from small sample sizes (Elith et al., 2006; Phillips et al., 2006). MaxEnt estimates the probable distribution of maximum entropy (i.e. closest to uniform) based on environmental variables dispersed over the areas to be surveyed (Pearson et al., 2007; Kaliontzopoulou et al., 2008).

Viperidae family (with subfamilies Azemiopinae: Fea's vipers, Crotalinae: Pit vipers, and Viperinae: True vipers) has more than 9.4% of all the living genera and species of the snakes (Uetz et al., 2023). The venomous snakes of the genus Macrovipera Reuss, 1927 (Type species: Coluber lebetinus Linnaeus, 1758) were distinguished and described from the genus Vipera Laurenti, 1768 by Herrmann et al., (1992) in order to include the large North African and Eurasian vipers (Cattaneo, 2020). The genus Macrovipera consists of two species as follows: M. lebetinus (Linnaeus, 1758), and M. razii Oraie, Rastegar-Pouyani, Khosrovani, Moradi, Akbari, Sehhati, Shafiei, Stümpel & Joger, 2018 which were geographically distributed in Morocco, Algeria, Tunisia, Cyprus, Syria, Lebanon, Jordan, Turkey, Iraq, Yemen (recorded by Scortecci 1932), Iran, Afghanistan, Pakistan, India (Jammu and Kashmir) (Leviton et al., 1992; Khan 2004; Stümpel & Joger, 2009; Uetz et al., 2023). The Levantine viper M. lebetinus is known with six recognized and valid subspecies: The
nominal subspecies Cypriot blunt-nosed viper *M. l. lebetinus* (Linnaeus 1758) seems to be endemic to Cyprus; the Cernov’s viper *M. l. cernovi* (Chikin and Szczerbak 1992) in Iran (Kerman, Khorasan Razavi, North Khorasan and Semnan Provinces), Afghanistan, Pakistan, Turkmenistan, Kyrgyzstan, Uzbekistan, India (Kashmir); the Levant blunt-nosed viper *M. l. obtusa* (Dwiguński 1832) in Lebanon, Jordan, Iraq, Syria, northeast Turkey, Transcaucasia, Iran (West Azerbaij an, East Azerbaijan, Ardabil, Qazvin, Gilan, Mazandaran, Golestan, Alborz, Tehran, Semnan, Qom, Markazi, Zanjan, Hamedan, Kurdistan, Kermanshah, Lorestan, Ilam, Khuzestan, Kohgiluyeh Va Boyer Ahmad, Fars and Esfahan Provinces), Afghanistan, Pakistan; the Milos viper *M. l. schweizeri* (formally *Viper schweizeri* Werner 1935) in Greece; *M. l. transmediterranea* (Nilson and Andrén 1988) in Algeria, Tunisia; and the Turan blunt-nosed viper *M. l. turanica* (Chernov 1939) in Tajikistan, Uzbekistan, Kyrgyzstan (Ananjeva et al., 2006; Jestrzemski & Kuzyakova, 2018; Uetez et al., 2022). According to the successful results of the hybridisation of the subspecies *schweizeri, lebetina, obtusa* and *turanica*, they have not raised the full species, because interbreeding has occurred between them (Kamelin et al., 1997).

In addition to the above-mentioned subspecies, there is also a challenging subspecies *M. l. peilei* (Murray, 1892), in Pakistan, which was rejected by the group of researchers (Golay et al., 1993; McDiarmid et al., 1999) and it is categorised as a synonym of *obtuse*, but according to Sindaco et al., (2013) *peilei* is synonymous with *M. lebetina cernovi*. Cattaneo (2020) investigated five species of *Macrovipera: lebetinus, razii, schweizeri, mauritanica and deserti* that *schweizeri, mauritanica* and *deserti* are considered subspecies of *lebetinus*, and Lenk et al., (2001) subcategorised *mauritanica* and *deserti* into the distinct genus *Daboia*, while other researchers are currently invalid (*euphratica, siphnensis*). The genus *Macrovipera* in the molecular phylogenetic aspect is a sister taxon of the mountain viper *Montivipera* Nilson, Tuniyev, Andrén, Orlov, Joger and Herrmann, 1999 (Lenk et al., 2001, Garrigues et al., 2005; Wüster et al., 2008; Stümpel & Joger, 2009; Pyron et al., 2013; Oraie et al., 2018). The general aim of this work is: 1) to identify model potential areas of distribution during three periods of the past: Last Interglacial (LIG: ~120,000–140,000 years BP) mid-Holocene (MH: ~6,000 years BP), 2) to describe present distribution, suitable habitat, and understand the biogeographical patterns of *M. lebetinus* in the World.

**Martial and methods**

**Study area and presence records**

The Levantine viper *M. lebetinus* (Fig. 1) can usually be found in the mountainous areas of Alborz
and Zagros and their adjacent areas, even in rural residential areas. This species is nocturnal and not very aggressive snake and it can also be seen in the early morning or at dusk. We collected the data concerning the species occurrence based on systematic biological survey by walking randomly through the habitat from 06:00 to 08:00 AM and 18.00-22:00 PM to evening (much of the activity time of species) during the spring to summer 2013 and 2021. We used localities mentioned in previous studies (e. g. Latifi, 1991; Disi et al., 2001; Khan 2002; Hraoui-Bloquet et al., 2002; Jablonski & Masroor, 2020). We gathered the data related to the distribution of *M. lebetinus* specimens collected in rodents’ nests, groove of rocks or around bushes of oak forest in the Zagros and Kopet Dag Mountains, near a poultry farm (Javanrod, Kurdistan Province) (Fig. 2) and recorded the exact location by using the Global Positioning System (GPS), and localities from the Global Biodiversity Information Facility (GBIF: https://www.gbi-f.org) website (GBIF 2022) were also included. In total, 140 records were gathered and used in this study.

![Fig. 1. Alive adult specimen of *Macrovipera lebetinus* in Zoology laboratory, Razi University (A); the camouflage of Levantine viper in its habitat (Tandoureh Protected Area northeast, near the city of Dargaz and the Turkmenistan border) (B and C).](image-url)
Fig. 2. Landscape of habitat of *Macrovipera lebetinus* in Pouyan Region, Kermanshah Province (A); Malle Punjab, Ilam Province (B); Bloran Region, Lorestan Province (C), and Tandoureh Protected Area, Khorasan Razavi Province (D).

**Data set and analysis**

We carried out the Maximum Entropy modeling (MaxEnt) using the software MaxEnt, 3.3.3e (Phillips et al., 2006) for surveying species geographic distributions and the data to test samples. In this study, 19 bioclimatic variables and two topographical variables were used for the contemporary time, and also 19 bioclimatic variables were used in the past time (LIG, and MH) in the species-related parts of the world (Eurasian and North African) (Hijmans et al., 2005; Otto-Bliesner et al., 2006; www.worldclim.org) (see the Appendix). To recognise the correlation ratios between variables and present records, Openmodeller (V. 1.0.7) (de Souza Muñoz et al., 2011), was used. Then, we used SPPS IBM (version 22) for Pearson’s correlation coefficient (Elith et al., 2006). We selected variables with a Pearson correlation lower than 0.75 to select the variables that are ecologically important for species separation according to our observations, in order for the habitat to be described.
We applied MaxEnt software and the analysis was repeated 15 times, yielding the best model for the studied species. Twenty-five percent of the data was used as test data, and the remaining percent of data (75 percent) was considered as training data. MaxEnt provides the distribution models by the receiver operating characteristic (ROC) plots, ROC curves plot true-positive rate against false-positive rates (Kaliontzopoulou et al., 2008). A value of 0.5–0.7 related to the area under the curve (AUC) indicates that the result is a stochastic prediction (Gallien et al., 2012), and values of 0.7–0.9 suggest an efficient model, the values more than 0.9 indicate high accuracy (Manel et al., 2001). We used DIVA-GIS 7.3.0.1 software for predicting the maps and a logistic output of present records with a suitability range showing the values of zero (unsuitable habitat) to one (the best suitable habitat) (Hijmans et al., 2001).

**Results**

The habitat suitability and distribution of the Levantine viper *M. lebetinus* were best described by a combination of bioclimatic and geographic variables suggested by a high value of the area under the curve (AUC) (LIG = 0.979± 0.008, MH = 0.968± 0.028, and contemporary period = 0.933± 0.036). The models showed a very significant match and closely fitted the presence of the species recorded in the studied areas. The contribution of different variables to different time periods is shown in Table 1. In the LIG model, the Mean temperature of the driest (19.7 ± 8.6 °C), and wettest (9.8 ± 5.3 °C) quarter of the year revealed more than half of the variance (61.7%); Therefore, temperature modality was the most important factor for the simulated distribution model during the LIG periods (Fig. 3A). In the MH model, maximum temperature of the warmest month (45.4 °C), and mean temperature of the wettest quarter of the year (10.2 °C) showed 61.6% of the variance. Also, the temperature was the most important factor for the simulated distribution models during the MH periods (Fig. 3B). In the contemporary model, seasonal and annual precipitation justified 32.9% and the slope accounts for 31.5% of the variance, where mean precipitation was 67-357 mm with slope 89° (Fig. 3C). The model for *M. lebetinus* predicated the occurrence range of the species in rocky hills, and mountain sides with an elevation of 3 to 2640 m above sea level (a.s.l.).
Table 1. Relative importance of variables (in percentages) in the last interglacial (LIG, ~120 ka), mid-Holocene (MH, ~6 ka), and the present period used in MaxEnt model for the Levantine viper *M. lebetinus*.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description of variables</th>
<th>LIG</th>
<th>MH</th>
<th>Present time</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bio9</td>
<td>Mean temperature of the driest quarter of the year</td>
<td>43.8</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bio5</td>
<td>Maximum temperature of the warmest month</td>
<td>-</td>
<td>36.4</td>
<td>-</td>
</tr>
<tr>
<td>Bio3</td>
<td>Isothermality [(BIO2 / BIO7) * 100]</td>
<td>26.9</td>
<td>21.2</td>
<td>11.5</td>
</tr>
<tr>
<td>Bio8</td>
<td>Mean temperature of the wettest quarter of the year</td>
<td>17.9</td>
<td>25.2</td>
<td>-</td>
</tr>
<tr>
<td>Bio15</td>
<td>Precipitation seasonality (standard deviation / mean)</td>
<td>9.4</td>
<td>12.9</td>
<td>16.5</td>
</tr>
<tr>
<td>Bio2</td>
<td>Mean diurnal range [mean of monthly (max temp – min temp)]</td>
<td>2.1</td>
<td>4.3</td>
<td>-</td>
</tr>
<tr>
<td>Slope</td>
<td>Slope</td>
<td>-</td>
<td>-</td>
<td>31.5</td>
</tr>
<tr>
<td>Bio12</td>
<td>Precipitation seasonality Annual precipitation</td>
<td>-</td>
<td>-</td>
<td>16.4</td>
</tr>
<tr>
<td>Bio4</td>
<td>Temperature seasonality (standard deviation * 100)</td>
<td>-</td>
<td>-</td>
<td>15.9</td>
</tr>
<tr>
<td>Altitude</td>
<td>Altitude</td>
<td>-</td>
<td>-</td>
<td>8.2</td>
</tr>
</tbody>
</table>
Discussion

Results of the present study verify the known distribution of the Levantine viper based on climatic conditions. The regions in the vicinity of the Mediterranean Sea, western Asia (the Middle East and the Caucasus), middle Asia (the plains and hills lying between the Caspian Sea to the west of China), south Asia (Afghanistan, Pakistan, and India) had a wide variety of area suitability for the presence of the Levantine viper during LIG, MH, contemporary periods. Climate change and habitat destruction (fragmentation and loss) are considered threats to global biodiversity (Travis, 2003; Opdam & Wascher, 2004). Climate changes followed by habitat destruction are the primary causes of the decline of reptiles globally and trigger the local extinction in many parts of the world. The habitat suitability such as northern Uzbekistan and Turkmenistan, southern and central Iraq, north Egypt and northeastern Libya have been lost for the Levantine viper over time; when habitat is lost, the populations of species are also likely to decline and disappear (e.g. Bender et al., 1998; Andrén, 1999; Mantyka-pringle et al., 2012). In the LIG, MH, contemporary periods, habitats in northern India and western Jordan had remained as patches with relatively low suitability (18 to 36%); the process of habitat fragmentation with increased number, isolation of patches and small populations increase the risk of extinction (Young et al., 1996; Mantyka-pringle et al., 2012). However, according to the models, the habitats of the west of the Caspian Sea have become more suitable for the Levant viper, and habitats such as southern Italy, Spain and Portugal were suitable in the three time periods, but until now there have been no report of the Levantine viper in the above-mentioned regions, which is possibly due to lack of access to those habitats. The Levantine viper inhabit in the very diverse desert and montane-steppe biotopes (Ananjeva et al., 2006) has made the viper to be able to tolerate climate change imposed on its habitats and continue to survive. Most records of the species occur in rock and dry foothills, on mountain slopes with sparse annual grasses, and thorny bushes, rocky ravines with small streams and springs, in pistachio and oak woodlands, on precipices in river valleys, on the banks of irrigation channels (Leviton et al., 1992; Ananjeva et al., 2006). The results of present study are consistent with all the previous records (e.g. Disi, et al., 2001; Ananjeva et al., 2006; Cattaneo, 2020) except the record of Yemen (a specimen collected in 1932 by Scortecci with uncertain locality), which was not suitable for inhabiting the Levantine viper during the LIG, MH, and contemporary periods. The results showed that the distribution of the Levantine viper is limited by different climatic parameters. Model distribution ranges during the MH to the present time indicated a gradual decline of habitat suitability in Morocco to northern India. During spring and summer, the increased
temperature and rainfall fluctuations over the regions show a clear decrease from the MH to contemporary time which can be elucidated by the changes in solar insolation due to the varying orbital force (Fallah et al., 2017). Park et al., (2019) reconstructed the annual mean Northern Hemisphere warming and Arctic amplification in response to Mid-Holocene insolation and also simulated the pronounced summer warming anomalies that persisted into winter. Terral & Mengüal (1999) suggested annual temperatures between 1.5°C and 3.5°C for southern Europe and the areas around the Mediterranean Sea (Molnar & Rajagopalan, 2020), which were cooler and wetter than the present time. Therefore, the MH had suitable climate conditions for the distribution of the Levantine viper from areas around the Mediterranean Sea to north India and west Kyrgyzstan. We think that temperature and precipitation, especially during spring and summer, are the most effective factors determining the habitat suitability for *M. lebetina*.

In addition to habitat change, fragmentation and decreasing connectivity between suitable habitats (small and isolated patches) lead to the interruption of gene flow among populations and, ultimately an increased extinction risk (Prugh et al., 2008; Fischer & Lindenmayer 2007; Ferraz et al., 2007; Spiesman et al., 2018). Three patterns are simulated for climate changes in our modelling: first, some suitable habitats almost disappear in the areas of climate change, as in northern Uzbekistan and Turkmenistan, southern and central Iraq, north Egypt and northeastern Libya; second, the vastness of suitable habitats reduces, as in Iran, Turkey, Syria, and Jordan; third, the suitability of some habitats increases, as in Azerbaijan, Armenia, and Dagestan. Consequently, climate change can cause the disappearance or reduction as well as the expansion of suitable habitats (Parmesan 2006; Bonino et al., 2015; Kim et al., 2020; Karamiani & Rastegar-Pouyani, 2021). Therefore, these regions might function as potential refuges for conservation of the species under the climate changes in the future.

**Conclusion**

The present study was carried out with the aim of modeling the potential distribution areas and determined the suitable habitats in the past (the Last Interglacial, and mid-Holocene), and current distribution of the Levantine viper by MaxEnt. Based on the results of this study can be firstly understand the decreasing trend of habitats with the effect of climate change from the past to the present, and secondly, to identify the range of distribution and habitats of the Levantine viper for can help to reduce the possibility of snakebite.
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References


evolution, 19(1), 94–104.


Appendix

Table 1. Climatic variables are used to elaborate the models (www.worldclim.org).

<table>
<thead>
<tr>
<th>Characters</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude</td>
<td>Altitude</td>
</tr>
<tr>
<td>BIO1</td>
<td>Annual mean temperature</td>
</tr>
<tr>
<td>BIO2</td>
<td>Mean diurnal range [mean of monthly (max temp - min temp)]</td>
</tr>
<tr>
<td>BIO3</td>
<td>Isothermality [(BIO2 / BIO7) * 100]</td>
</tr>
<tr>
<td>BIO4</td>
<td>Temperature seasonality (standard deviation * 100)</td>
</tr>
<tr>
<td>BIO5</td>
<td>Maximum temperature of the warmest month</td>
</tr>
<tr>
<td>BIO6</td>
<td>Minimum temperature of the coldest month</td>
</tr>
<tr>
<td>BIO7</td>
<td>Temperature annual range (BIO5 - BIO6)</td>
</tr>
<tr>
<td>BIO8</td>
<td>Mean temperature of the wettest quarter of the year</td>
</tr>
<tr>
<td>BIO9</td>
<td>Mean temperature of the driest quarter of the year</td>
</tr>
<tr>
<td>BIO10</td>
<td>Mean temperature of the warmest quarter of the year</td>
</tr>
<tr>
<td>BIO11</td>
<td>Mean temperature of the coldest quarter of the year</td>
</tr>
<tr>
<td>BIO12</td>
<td>Annual precipitation</td>
</tr>
<tr>
<td>BIO13</td>
<td>Precipitation of the wettest month</td>
</tr>
<tr>
<td>BIO14</td>
<td>Precipitation of the driest month</td>
</tr>
<tr>
<td>BIO15</td>
<td>Precipitation seasonality (standard deviation / mean)</td>
</tr>
<tr>
<td>BIO16</td>
<td>Precipitation of the wettest quarter of the year</td>
</tr>
<tr>
<td>BIO17</td>
<td>Precipitation of the driest quarter of the year</td>
</tr>
<tr>
<td>BIO18</td>
<td>Precipitation of the warmest quarter of the year</td>
</tr>
<tr>
<td>BIO19</td>
<td>Precipitation of the coldest quarter of the year</td>
</tr>
<tr>
<td>Slope</td>
<td>Slope</td>
</tr>
</tbody>
</table>